Acta Biol. Szeged. 31, pp. 55—69 (1985)

EFFECTS OF ENVIRONMENTAL FACTORS ON ION UPTAKE BY PLANTS*

F. ZSOLDOS

(Received: July 1, 1984)

Introduction

Environmental factors such as temperature, oxygen supply, pH, etc. considerably affect the ion uptake by plants, hence the mineral nutrition. Detailed investigations of these factors are therefore of importance from both theoretical and practical aspects.

The concept of environmental factors has to a certain extent been widened by the intensive chemicalization of agriculture in recent years, without which modern plant production would hardly be imaginable. The herbicides used in chemical weed control not only destroy weeds, but also influence the metabolism of plants and thereby the yield. Thus besides the classical environmental factors, but because of the possible interactions with them, the individual and general physiological effects of some biologically active substances must be studied. This is necessary for the safe use of the chemically active substances that are indispensable in modern crop production and for the protection of the environment and the biosphere.

The mineral nutrition of plants, or more precisely the uptake of ions, has been especially intensively studied during recent decades, and many valuable data are available for practice too (EPSTEIN, 1972; MENGEL and KIRKBY, 1978). Unfortunately, it can not be said that the mechanism of uptake of nutrients is sufficiently clarified in detail. The research work and the establishment of general regularities are made more difficult by the fact that the differences in uptake of some nutrient elements due to the influence of environmental factors may vary markedly with the plant species (EPSTEIN, 1972; LÜTTGE and PITTMAN, 1976).

Ion uptake by plants can be classified phenomenologically on the basis of the Q_{10} value into two main processes: in one case the Q_{10} value is generally about 1.0—1.2, while in the other it is 2—3 or even higher (SUTCLIFFE, 1962). In the former case the ion uptake is regulated chiefly by physical processes, e.g. diffusion, mass flow, exchange and the passive processes connected with these. In contrast, in the latter case ion uptake occurs primarily in connection with the metabolism, and we therefore speak about an active mechanism.

The effects of environmental factors on these two mechanisms are very different, and depend on the characteristics of the element involved. In general, the effects of temperature, pH and O_2 conditions, but also various biologically active

* Based on an academic doctoral dissertation defended on January 7th, 1983.

compounds, operate, mediated by the metabolically regulated transport processes. If the effects of the environmental factors are not too high the transport processes connected with the metabolism will not be seriously impaired. The reverse of this is true in the case of extreme and sudden changes. There is generally then a stress effect, that may lead directly or indirectly to damage to the membrane and to impairment of the metabolic processes, cell structures, and ion transport connected with the membrane (LEVITT, 1972).

The temperature is an important environmental stress factor from a practical point of view (LYONS et al., 1979). However, the effects of pH and the different biologically active substances, e.g. herbicides, must also be taken account (CARSON, 1974; Audus, 1976). All these factors were considered in the design of our research programme and in the selection of the test plants too.

The importance of the temperature and pH effects has been known for a long tíme but in spite of this both theoretically and practically important questions, especially in connection with thermophilic plants, have not yet been cleared up satisfactorily (LYONS et al., 1979). This is one reason for the fact that endeavours to clarify the consequences of cold damage to thermophilic plants or the consequences of low temperature on the mineral nutrition of plants are still in the initial stage. As concerns the pH effects, the data relating to the different plant species are insufficient and very general. The situation is very similar for some biologically active compounds. In this connection, the herbicides are worthy of special attention; under different environmental conditions, chiefly conditions of temperature and pH, these compounds may influence the mineral nutrition of cereals in very different ways.

Materials and methods

Our investigations were carried out on crops more or less sensitive to environmental factors. One reason for the selection of thermophilic rice as one test plant was the thought that this research might promote the solution of the special and difficult task of Hungarian rice cultivation. It is true that there are a few special traits in the mineral nutrition of rice plants, but some generally known ion uptake processes are to be considered too (FRIED et al., 1965). Another important test plant was wheat a well-known non-thermophilic crop that is especially convenient for comparative investigations. We also investigated other thermophilic plants (e.g. sorghum, cucumber, corn, grapes), to assess the possibility of generalizing conclusions.

Our investigations were made predominantly with the roots of young plants grown in water cultures under controlled conditions. In the investigations of mineral nutrition, the internationally accepted methods were kept in view. Accordingly the low-salt plants were grown in a solution containing 0.5 mM $CaSO_4$. The controlled conditions were insured partly with Conviron, and partly with Vötsch growth chambers.

The short ion transport experiments (influx, efflux), if not mentioned otherwise, relate to a 1 h experiment time. The uptake solution was in general 1 mM. In the case of herbicide treatment, the concentration is given for the active ingredient.

Ion uptake was followed mainly with a tracer technique. Stable and radioactive isotopes were applied in the experiment. Other methods too were used (e.g. atomic absorption spectrophotometry, flame spectrophotometry, etc.).

Measurements on the stable isotope N-15 were made partly in the IAEA Laboratory, and partly in the Austrian Research Centre Laboratory in Seibersdorf. N-15 was determined according to the modified Dumas method developed in the laboratory in Seibersdorf.

The results were generally evaluated through the joint consideration of several data, e.g. ion influx and efflux, and moreover the changes in the quantities of different mineral nutrient and free amino acid contents. As the changes in growth show the reversibility or irreversibility of changes at the cell level, we took this into consideration in the evaluation of stress effects.

The laboratory investigations were occasionally complemented with the results obtained in field experiments at the Research Institute for Irrigation, Szarvas, and the Cereal Research Institute, Szeged, Hungary.

In the experiments relating to the effects of herbicides, the following chemicals were used: Aniten D (2,4-dichlorophenoxyacetic acid+9-hydroxyfluorene-9-carboxylic acid butyl ester); Dikonirt (2,4-dichlorophenoxyacetic acid); Gabonil (4-chloro-2-methylphenoxyacetic acid+3,6-dichloro-2-methoxybenzoic acid); Saturn (S-4-chlorobenzyl-N,N-diethyl-thiolcarbamata); Synpran N (3,4-dichloropropionanilide); Synpran 111 (3,4-dichloropropionanilide+2, 4, 5-trichlorophenoxyacetic acid).

As our investigations with different herbicides soon demonstrated that the physiological effects of auxin-type herbicides to a particularly large extent we initially concentrated our attention on this problem.

Naturally, the still open problems connected with this question are so wide-ranging that a consideration of all their aspects is beyond the limitations of the present discussion. Our investigations were therefore limited to the first steps of mineral nutrition, i.e. to individual relations of the mineral nutrient uptake by roots, and in certain cases only to the study of K^+ uptake.

The key role of K^+ in the maintenance of the structure and physiological functions is well known (International Potash Institute, 1971). At the same time, the data relating to K^+ uptake, and the changes of its transport due to the effects of environmental factors are rather sparse. As the bulk of K^+ occurs in ionic form in plant cells, for this element the effects of stress factors can be taken into account to a higher degree than for other nutrients. This prompted us to devote special attention to a study of the effects of the environmental factors on K^+ transport (influx, efflux).

During our investigations we dealt with the effects and interactions of some environmental factors, primarily the temperature and pH conditions, and also some biologically active substances (herbicides) influencing the uptake of nutrients by rice and wheat seedlings. Thus, the chief aims of this work extend to the following three closely connected topics:

1. Comparative investigations of the ion uptake and growth of thermophilic and non-thermophilic plants, with special attention to
   - the K^+ uptake occurring in connection with a sudden fall in temperature, and its distribution along the various root segments;
   - the mechanism of ion uptake stimulated by Ca^{++};
   - the structural and growth alterations of cell membranes, caused by a short treatment at low temperature.
2. Study of the effects of the ion uptake and growth, with special attention to
   - the uptakes of K^+, NH_4^+ and NO_3^-;
   - the direct and indirect damaging effects of extreme H^+ concentrations and the role of Ca^{++} in connection with membrane transport stabilization.
3. Study of the interactions between herbicide treatment and some environmental factors, with special attention to
   - the ion uptake by the roots (root zones);
   - the connection between specific herbicide sensitivity and ion uptake;
   - the interactions between pH and the different types of herbicides.

Summary of new scientific results

1. The effects of a sudden fall in temperature (cold stress) on the ion transport of thermophilic and non—thermophilic plants

1.1. The roots of thermophilic plants show a K^+ uptake (influx) anomaly following a sudden fall in temperature. Consequently, the K^+ influx is considerably higher than would be expected at and near 0 °C.

1.2. As an effect of cold stress, a high-temperature K^+ uptake anomaly can also be demonstrated for thermophilic plants. In this case the K^+ uptake in the physiological temperature range of the plants will be increased by about 50% for a short time. This phenomenon can not be detected with other essential elements or with non-thermophilic plants.

1.3. Similarly to the influx anomaly an efflux anomaly may also be detected: the roots of thermophilic plants lose a considerable quantity of K^+ into the outher medium at low temperature. As concerns the essential elements, the anomaly can be detected only for K^+, and is characteristic only of thermophilic plants (roots).

1.4. At low temperature (10—12 °C) the uptakes of some nutrients may differ considerably: the uptakes of NO_3^- and $H_2PO_4^-$ are much more inhibited than that of NH_4^+, for instance.

2. Anomalous K^+ transport and its characteristics

2.1. The anomalous K^+ uptake appears in a considerably increased absorption process with negative temperature coefficient, the occurrence of which depends critically on the rate of fall of temperature. In the case of gradual coolling, the anomalous K^+ influx is moderated and may eventually cease to come about.

2.2. The concentration of the uptake solution has a marked influence on the absolute value of the influx and on the change with temperature.

2.3. The anomalous K^+ influx is not basically influenced by an uncoupler (e.g. 2,4-DNP), or by a respiration inhibitor. In contrast, however, the pH of the uptake solution and its Ca^{++} content have considerable effects on the process; e.g. under pH 5.5, or in the presence of a certain concentration of Ca^{++}, the anomaly practically ceases.

2.4. There is a close connection between the measure of the influx anomaly and the length of the root (or more exactly its age): the shorter (younger) the root the more expressed the anomaly.

2.5. A correlation can be demonstrated between the low-temperature K^+ influx anomaly and the differing cold sensitivities of some thermophilic species: the more cold sensitive a species, the more intensive the anomalous K^+ influx for a given period of time.

3. The distribution of anomalous K^+ influx along the roots

3.1. The anomalous K^+ influx is restricted to a definite root zone, e.g. exclusively the apical zone in the case of rice, whereas with cucumber — because of the extremely long root calyptra — it is the second 1 cm segment from the apex.

3.2. If the Ca^{++} concentration of the uptake solution reaches a certain value the K^+ influx decreases in all root segments, but especially in the apical meristematic zone.

3.3. At higher temperatures, but still within the physiological temperature range, for both thermophilic and non-thermophilic plants the K^+ influx is the lowest in the apical zone.

4. Studies of ion interaction with special attention to the role of Ca^{++} (Viets effect)

4.1. The degree of Ca-stimulated K^+ uptake (Viets effect) for rice and wheat under low-salt conditions differs, depending on the root segment and the plant species too. Development of the Viets effect is considerably influenced by the Ca^{++}/K^{+} relation and by the ion strength of the uptake solution.

4.2. The Viets effect can be demonstrated only in the range of physiological temperature needed by the plant. For rice this is from 14 to 40 °C, while for wheat it is from 7 to 30 °C.

4.3. The K^{+} uptake is considerably inhibited by NH_4^+, but the NH_4^+ uptake is not influenced by K^{+}. A high (10 mM) concentration of Na^{+} stimulates K^{+} uptake in the presence of Ca^{++}.

4.4. As concerns the essential elements, the Viets effect was experienced in the uptake of $H_2PO_4^-$ at lower temperatures too, while for NH_4^+ and NO_3^- in the presence of Ca^{++} a smaller inhibitory effect was observed.

5. The distribution of potassium and calcium along the root, and its role in the process of K^{+} uptake

5.1. At low temperature (0 °C) in a Ca-deficient uptake solution, the K^{++} content of rice roots definitely decreases. In the presence of Ca^{++}, chiefly the K^{+} loss (leakage) of the apical meristematic zone increases further and may reach 30—40%. With the non-thermophilic wheat under similar experimental conditions, only an insignificant K^{+} loss appears.

5.2. For rice roots kept in Ca-deficient uptake solution, a K^{+} loss can be detected at higher temperature (25 °C), while for wheat this is not experienced; there is even a net K^{+} uptake without Ca^{++}.

5.3. In the range of physiological temperature, a Ca-stimulated net K^{+} uptake, i.e. a Viets effect, can be demonstrated along the root segments for both thermophilic and non-thermophilic plants. In the apical meristematic region, however, presumably on account of the very high K^{+} concentration, this effect does not appear, or to only a very moderate extent.

5.4. The Ca contents of all root segments increases considerably at 0 °C and 25 °C, compared to the untreated control, for both thermophilic and non-thermophilic plants. For thermophilic plants at low temperature, however, there is an essentially higher Ca content in the zone showing a K^{+} influx anomaly.

6. The effects of cold stress on the growth of rice and wheat

6.1. Brief cooling of thermophilic plants to 0 °C causes a growth disturbance indicative of damage to the root apical meristematic zone. In roots exposed to the cold stress effect, a considerable structural change and disorganization results after 2—3 days. As a consequence of cold treatment, the root hairs and the underlying 4—5 cell layers of the primary cortex die. At the same time, we could detect no changes in the stele of the roots.

6.2. On the third day after cold treatment the development of side-roots from the one-layer pericycle started at many places. This differed from normal side-root development, however: the supplementation of the decayed tips began in the root-hair zone, and the cell division started simultaneously at more places than under normal conditions.

6.3. The regeneration of cold-treated roots is completed when basiton-type roots are observed externally too, about 14—16 days after cold stress. This phenomenon cannot be observed with the other group (in our case winter wheat) under the same experimental conditions.

7. The effects of pH (H^+ stress) on ion uptake and growth of roots

7.1. With rice at low pH, a K^+ uptake anomaly (influx) can be demonstrated, as a result of which the K^+ influx increases considerably at such concentrations. With wheat under similar experimental conditions, this effect is not noted; increase of the H^+ concentration results in a monotonous decrease of uptake.

7.2. The irregular K^+ influx stimulated by H^+ stress does not result in a net ion uptake; even under such conditions, a K^+ leakage can be noted. The K^+ influx anomaly, made possible by an ion-exchange process, is highly influenced by the ion composition and (predominantly Ca^{++}) the concentration of the uptake solution.

7.3. In the uptakes of NH_4^+, NO_3^- and $H_2PO_4^-$ ions, a pH-stimulated anomaly can not be detected for either rice or wheat. The uptakes of these ions proceed as expected.

7.4. The growth of rice and wheat between pH values of 5 and 10 is undisturbed. Unexpectedly, more extreme (acidic or alkaline) pH conditions are tolerated better by rice than by wheat. As with cold stress, sudden changes play an important role in this case too.

8. The effect of herbicides on the nutrient uptake by roots

8.1. Low (10^{-6}—10^{-8} M) herbicide concentrations are generally stimulatory, while higher ones (1.0—0.1 mM) have inhibitory effects. For both inhibition and stimulation, however, important differences are noted for certain nutrients. Our investigations showed the K^+ and NO_3^- uptakes to be much more sensitive to herbicide treatment than those of NH_4^+ or $H_2PO_4^-$.

8.2. At higher herbicide concentrations (1.0—0.1 mM), the cell membrane can be directly damaged, which causes considerable ion and free amino acid leakage.

8.3. A pH decrease strongly increases the uptake of auxin-type herbicides, and hence the disturbing effects of their ion uptake and growth inhibition. For non-auxin-type herbicides, the change of pH does not influence the phytotoxic effects of the compounds.

8.4. The temperature coefficient (Q_{10} about 1.7) of 2,4-D uptake and the accumulation of 2,4-D experienced in the roots suggest that the initiated influx of auxin-type compounds may be a process requiring energy.

8.5. Even at a concentration of 0.01 mM, auxin-type herbicides cause a considerable growth disturbance, primarily in the roots. The roots are more sensitive than the shoots to auxin herbicides. The reduction in the root growth was not in accordance with the dry matter production or mineral content: the higher the growth disturbance, the higher the mineral content in the root.

9. COMPARATIVE INVESTIGATIONS OF HERBICIDE SENSITIVITY

9.1. Following different herbicide treatments, marked differences can be observed in the ion uptakes of wheat and rice roots and root segments. With increase of temperature, the inhibitory effects of herbicides on the ion transport and growth of plants, especially thermophilic rice, increase.

9.2. Some crops show different sensitivities to different herbicides as concerns ion uptake, growth and dry matter production. The GK 3 wheat species, for instance, is less sensitive to 2,4-D than to MCPA treatment, while in the case of the Rannaja 12 species the reverse is true. The Dunghan Shali rice species is much more sensitive than Szarvasi 70 to 2,4-D.

9.3. At higher temperatures, 0.1—0.01 mM herbicide generally decreases the ion uptake of all root zones, while at low temperatures the uptake system of the older (more differentiated) zones is damaged.

9.4. 2,4-D uptake by rice roots and its transport to the shoots is faster than in wheat. This may partly explain the different herbicide sensitivities experienced for some crops. At low temperatures (for wheat, 5 °C, for example) the uptake (transport) and unfavourable physiological effects of herbicides practically cease.

New basic results and their practical importance

1. Depending on the K^+ influx response to a sudden fall of temperature (cold stress), plants can be divided into two main groups. Those thermophilic at or near 0 °C show an anomalous K^+ influx, while this is not characteristic for the non-thermophilic group. Our investigations so far suggest that the K^+ influx anomaly resulting from passive ion-exchange is one of the determining features of thermophilic plants.
2. There is a definite relation between the cold resistance of thermophilic seedlings and the extent of the K^+ influx anomaly. Measurements of changes in K^+ influx due to exposure to low temperature can therefore be used to estimate varietal differences in cold-resistance: a test procedure is proposed for the screening of newly bred or newly introduced thermophilic varieties for temperature-sensitivity.
3. Under acidic stress conditions, roots of thermophilic plants undergo changes in plasma membrane composition and structural organization, resulting in a K^+ influx anomaly and leakage. The K^+ influx and K^+ content data indicate that, under these conditions, cytoplasmic K^+ readily exchanges with labelled K^+(^{86}Rb) in the presence of zero or low Ca^{++} concentration.
4. Ca^{++} not only eliminates the K^+ uptake anomaly but reverses the anomalous K^+ influx. From the above facts it can be concluded that the K^+ uptake anomaly is a phenomenon connected primarily with the plasmalemma of roots, i.e. there must be an essential difference between the thermophilic and non-thermophilic plant root cells as concerns the composition and/or structure of the plasmalemma.
5. The transport characteristics and ion transport relations of the plant roots are heterogeneous. The marked (3—4-fold) K^+ concentration gradients between the root segments (apical zone and differentiated zones) show that chiefly metabolic processes take part in their maintenance.

6. Under stress effects a considerable leakage of different nutrients, and primarily K^+, must be taken into account. Under such conditions, therefore, or later, mainly those organs (root zones) are damaged which use a relatively high K^+ concentration for the normal physiological functions. It is not surprising that for thermophilic plants, e.g. in the effect of cold stress, (irreversible) changes occur in the apical meristematic zone that lead to the disorganization (death) of the root apex, the cessation of elongation growth and irregular side-root development. All this repeatedly draws attention to the especially important physiological function of K^+.
7. To arrive at a correct understanding of the mechanism of ion uptake by roots, it is absolutely necessary to take into consideration the different behaviours of some root zones. The varied behaviour of the root zones at low temperature, and especially that of the apical meristem, deserves special attention from both a methodical and a general physiological point of view.
8. The effects of auxin-type herbicides on ion uptake and transport (and hence growth) depend critically on the pH. Their proper application therefore demands a consideration of the chemical properties of the soil.
9. As concerns the uptakes of different nutrients, important differences can be observed between plant species on the action of herbicides. This condition must be taken into account in solving actual tasks connected with agrochemical processes (fertilizing, chemical weed control, etc.). This is especially so for thermophilic plants that are exceptionally sensitive to different environmental stress effects (sudden changes).

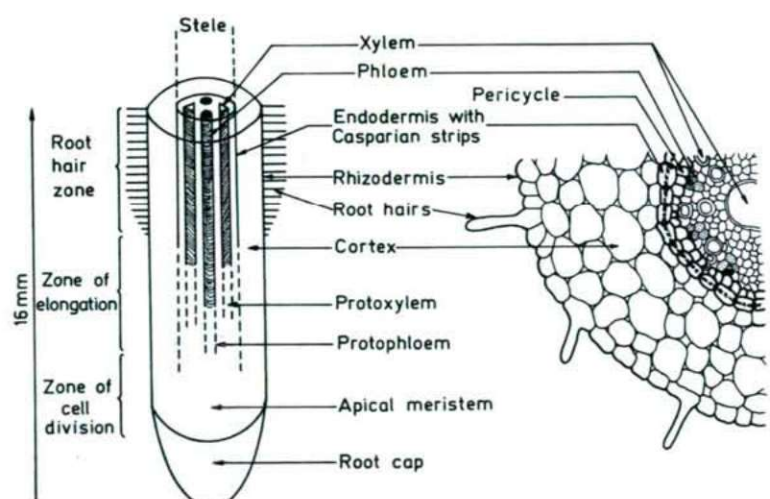

Fig. 1. Root anatomy. A) Diagram of a root tip showing the spatial relations of different tissues and order of maturation. B) Cross-section of a root of a monocotyledon. (Modified after ESAU 1969).

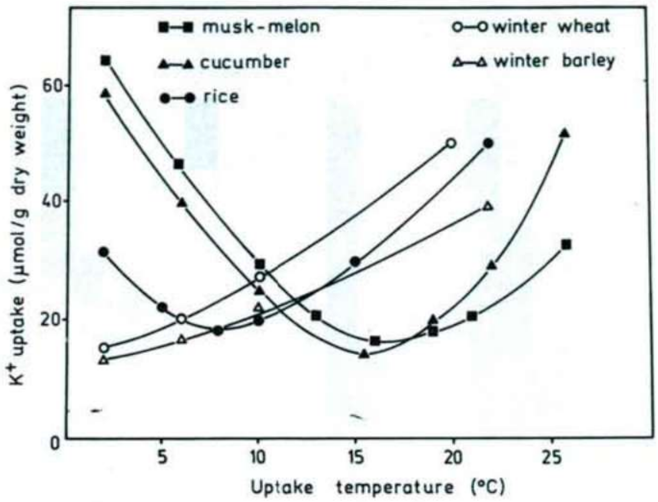

Fig. 2. Temperature-dependence of initial K^+(^{86}Rb) uptake by excised roots of various plants after sudden cooling of the uptake temperature. Absorption solution: 0.5 mM KCl; uptake time: 50 min. (Connected sections: 1.1, 1.4, 2.1, 2.5; and publications: 1, 3, 5, 13, 32, 35).

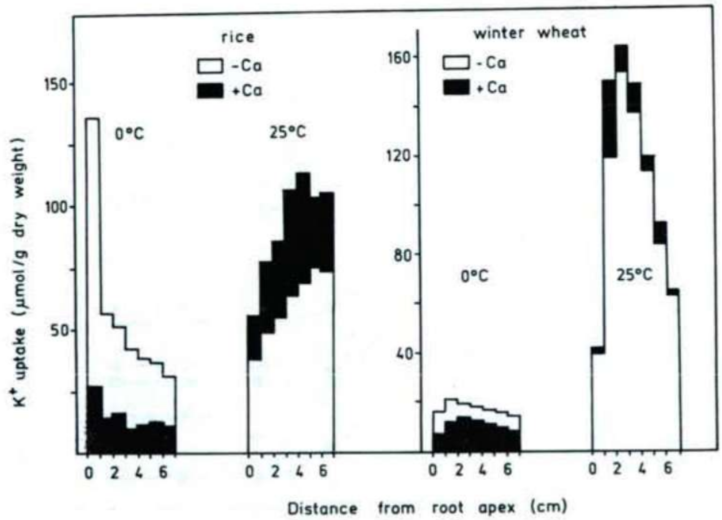

Fig. 3. Effects of Ca^{2+} and temperature upon K^+(^{86}Rb) uptake distribution patterns along primary roots of rice and winter wheat. Absorption solution: 1 mM KCl with or without 1 mM $CaCl_2$; uptake time: 60 min. (Connected sections: 3.1, 3.2, 3.3, 4.1; and publications: 17,18, 25, 26, 32).

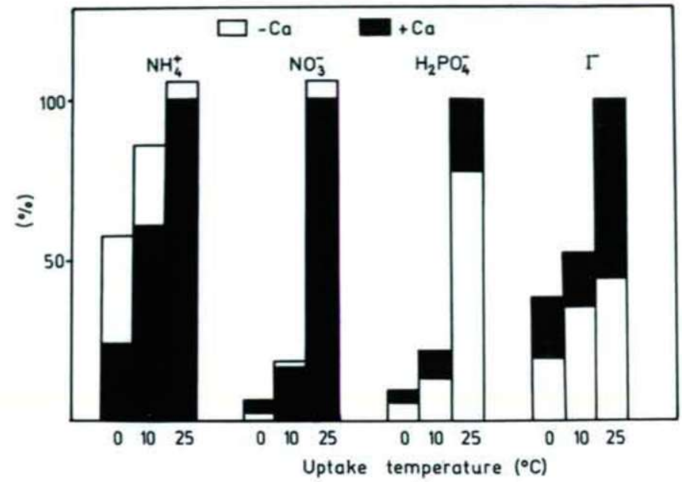

Fig. 4. Temperature-dependence of initial uptake of different ions by excised rice roots after sudden cooling to the uptake temperature. The labelled absorption solution contained 0.5 mM of NH_4Cl, $NaNO_3$, NaJ each and 0.1 mM KH_2PO_4, respectively. Uptake time: 60 min. (Connected sections: 1.4, 4.4; and publications: 9, 12, 32).

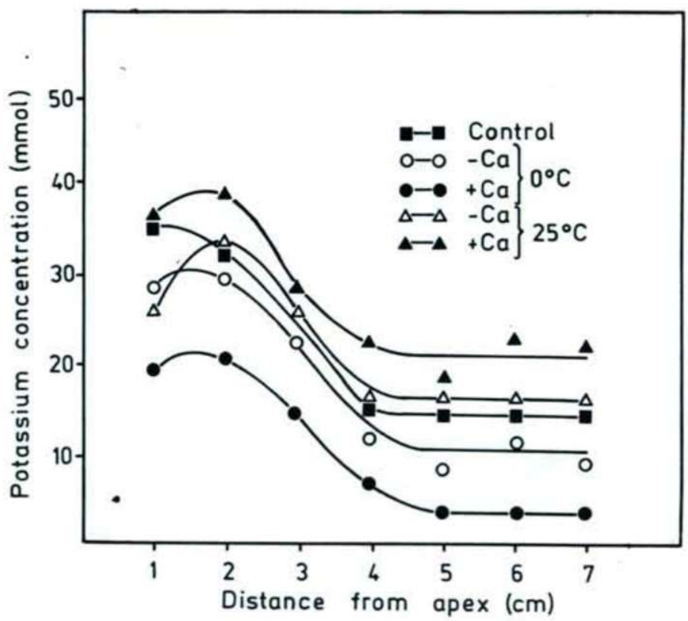

Fig. 5. Concentration distribution of K^+ along rice root (ORYZA SATIVA *L.* cv. *Dunghan Shali*) in the presence and absence of Ca^{2+} at 0 and 25 °C. Otherwise as in Fig. 3. (Connected sections: 5.1, 5.2, 6.1, 6.2, 6.3; and publications: 29, 30, 34, 35, 36, 37).

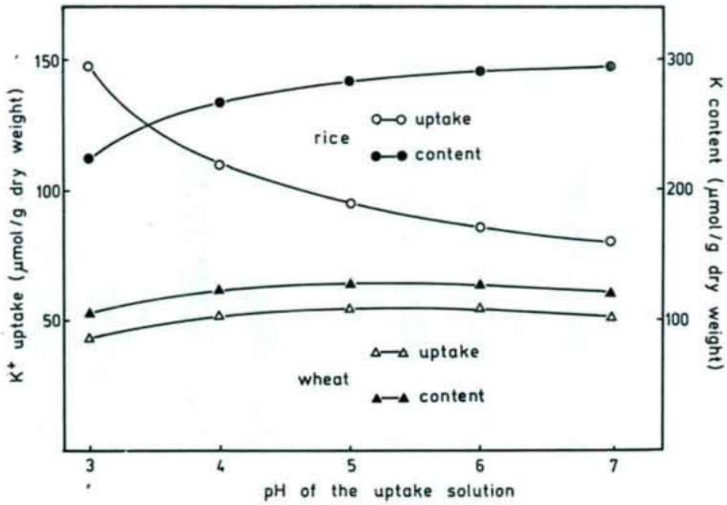

Fig. 6. Effect of pH on K^+(^{86}Rb) uptake and K^+ content of excised rice and winter wheat roots. The uptake solution contained 1 mM KCl+0.5 mM $CaCl_2$; otherwise as in Fig. 3. (connected sections: 7.1, 7.2; and publications: 34, 35, 36, 37).

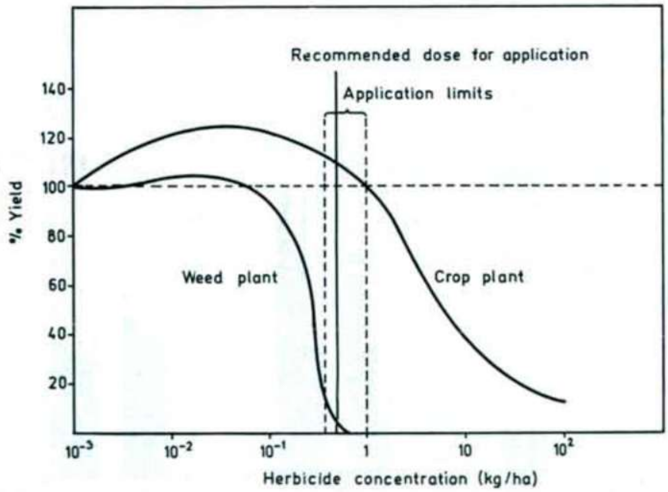

Fig. 7. The influence of different doses of a herbicide on the yield of crop plant and weeds. After LINSER (1976). (Connected sections: 8.1, 8.2, 8.5; and publications: 15, 19, 22, 24, 27, 28, 29, 31, 36).

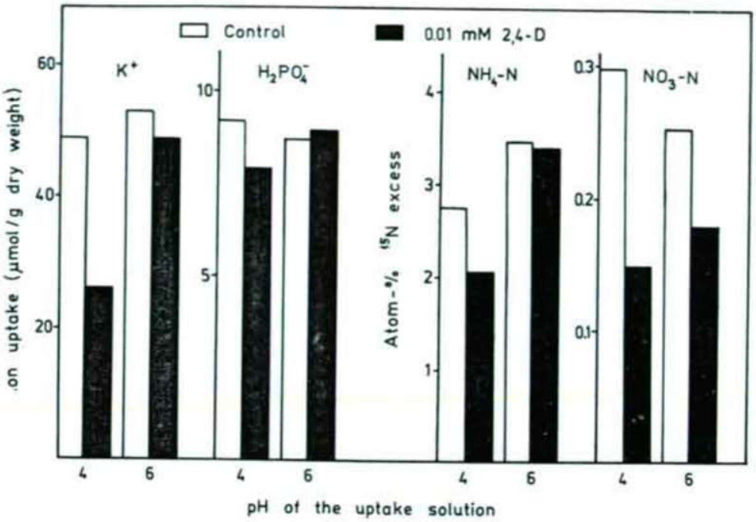

Fig. 8. The effect of 2,4-D on the uptake of K^+, $H_2PO_4^-$, NH_4^+ and NO_3^- ions of rice roots at different pH values. The uptake solution contained 1 mM $K(^{86}Rb)Cl + 0.5$ mM $CaCl_2$; $^{15}NH_4Cl + 0.1$ mM $CaSO_4$; $Na^{15}NO_3 + 0.1$ mM $CaSO_4$ each and 0.1 mM $KH_2{}^{32}PO_4 + 0.5$ mM $CaCl_2$, respectively. Otherwise as in Fig. 3. (Connected sections: 8.1, 8.3, 8.4; and publications: 27, 30, 36).

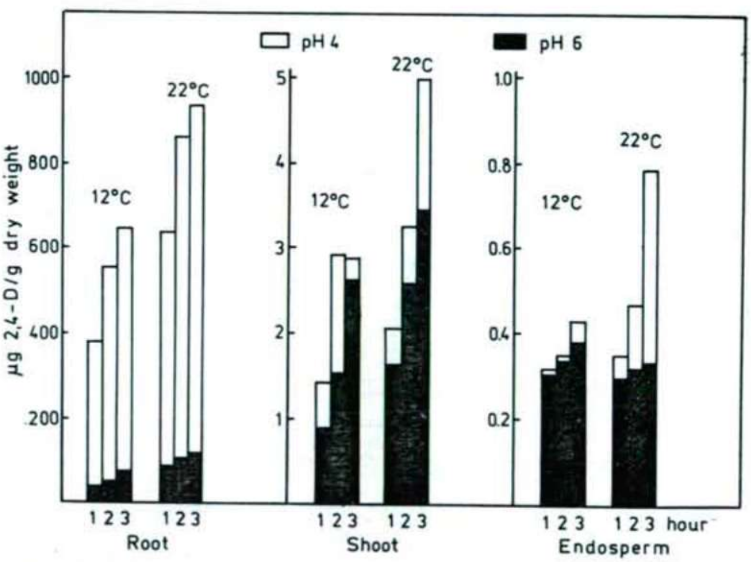

Fig. 9. The effects of pH on the uptake of 2,4-D and its transport within rice seedlings. The uptake solution contained 0.01 mM ^{14}C-2,4-D + 0.5 mM $CaCl_2$. The uptake time was 1, 2 and 3 h. (Connected sections: 8.4, 9.1, 9.3; and publications: 29, 30, 36).

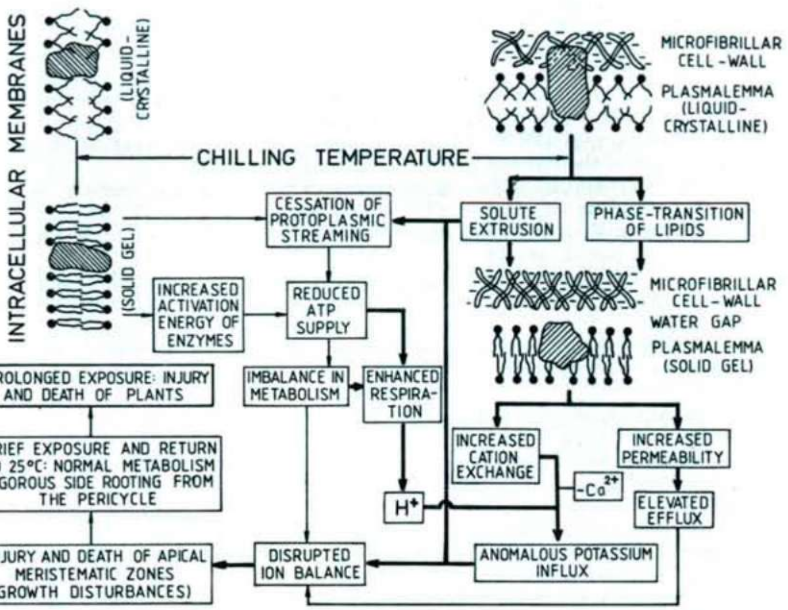

Fig. 10. Suggested schematic pathway of membrane-linked events involved in chilling injury of the apical meristematic zones of thermophilic plant roots. The model is an extension of that proposed originally by LYONS (1973).

Selected publications relating to the dissertation

ZSOLDOS, F. (1967): Alacsony hőmérséklet hatása a rizsgyökerek ionfelvételére. (Effect of low temperature on the ion uptake by rice roots). — Agrokémia és Talajtan *16,* 653—658.

ZSOLDOS, F. (1967): The ion uptake of rice roots at different pH values. — Acta Biol. Szeged. *13,* 113—118.

ZSOLDOS, F. (1968): Uptake of rubidium ion in different plant exposed to sudden fall in temperature. — Z. Pflanzenernähr. Bodenkunde *119,* 169—173.

ZSOLDOS, F. (1968): The effect of different factors on the rubidium ion uptake by roots under low temperature. — Z. Pflanzenphysiol. *60,* 1—4.

ZSOLDOS, F., CSEH, E. and BÖSZÖRMÉNYI, Z. (1968): Potassium and bromide uptake by excised roots at different temperatures. — Z. Pflanzenphysiol. *60,* 75—77.

ZSOLDOS, F., SIROKMÁN, F. and CSEH, E. (1969): Rubidium uptake and exchange of roots influenced by low temperature and some inhibitors. — Z. Pflanzenphysiol. *60,* 169—171.

ZSOLDOS, F. (1969): Effect of low temperature on the ion uptake by rice roots. — Acta Agron. Hung. *18,* 121—126.

ZSOLDOS, F. (1970): The influence of pH and temperature on rubidium/potassium ion absorption and exchange by roots. — Z. Pflanzenernähr. Bodenkunde *126,* 210—217.

ZSOLDOS, F. (1971): Ammonium and nitrate ion uptake by plants. — In: Nitrogen-15 in Soil-Plant Studies. Int. Atomic Energy Agency, Vienna pp. 81—89.

ZSOLDOS, F. (1971): Isotope technique for investigations of cold resistance in rice and sorghum varieties. — Plant and Soil *35,* 659—663.

ZSOLDOS, F. (1972): The influence of environmental factors and physiologically active substances on the ion uptake of roots. — Int. Atomic Energy Agency, Vienna. Res. Contracts, Ann. Rep. Techn. Ser. No. *134,* 72—74.

ZSOLDOS, F. (1972): Ion uptake by cold-injured rice roots. — Plant and Soil *37,* 469—478.

ZSOLDOS, F. (1974): Temperature-dependence of potassium uptake by roots. — In: Potassium Research and Agricultural Production. Int. Potash Inst. Berne pp. 167—174.

ZSOLDOS, F. (1974): Uptake and efflux of ions in fungicide treated rice plants. — Plant and Soil *41*, 41—49.

ZSOLDOS, F. and MÉCS, P. (1974): Ion uptake and cellmembrane behaviour of Synpran N and Dacthal herbicide treated rice plants. — Acta Biol. Szeged. *20*, 115—120.

ZSOLDOS, F. and KARVALY, B. (1975): Effect of temperature and concentration on the anomalous potassium uptake of thermophilic plants. — Experientia *31*, 75—76.

ZSOLDOS, F. (1975): Dependence of potassium uptake of rice and wheat seedlings on temperature, presence of calcium ion and root length. — Acta Biol. Szeged. *21*, 83—87.

ZSOLDOS, F. (1975): Potassium uptake along roots of thermophilic plants at different temperatures. — Plant Physiol. Suppl. *56*, 43.

ZSOLDOS, F. (1975): Herbicidek túladagolásának növényfiziológiai hatásai. (Plant physiological effects of overdosed herbicides). — Csongrád megyei Környezetvédelmi Ankét. Szeged, pp. 177—187.

ZSOLDOS, F. (1975): A revised isotope technique for investigation of cold-resistance in rice varieties. — Newsletter on the Application of Nuclear Methods in Biology and Agriculture, No. *5*, 18—19.

ZSOLDOS, F., KARVALY, B. and TÓTH, I. (1976): Na^+ stimulated K^+ uptake in different plant roots. — Plant Physiol. Suppl. *57*, 85.

HAUNOLD, E. und ZSOLDOS, F. (1976): Der Einfluss von 2,4-D und MCPA auf die Aufnahme und Abgabe von $^{86}Rb(K)$ und ^{32}P durch Weizenwurzeln. — Die Bodenkultur *27*, 331—338.

ZSOLDOS, F., TÓTH, I. and ERDEI, L. (1977): The effects of 2,4-D and MCPA on the ion transport processes of roots under different environmental conditions. — Plant Physiol. Suppl. *59*, 124.

ZSOLDOS, F. and HAUNOLD, E. (1977): Studies of herbicide sensitivity in the uptake of different ions by rice roots. — Acta Biol. Szeged. *23*, 63—67.

ZSOLDOS, F. and KARVALY, B. (1978): Effects of Ca^{++} and temperature on potassium uptake along roots of wheat, rice and cucumber. — Physiol. Plant. *43*, 326—330.

ZSOLDOS, F. and KARVALY, B. (1978): Effects of Ca^{++} and temperature on potassium content along roots of wheat, rice and cucumber. — Physiol. Plant. *43*, 331—336.

ZSOLDOS, F., KARVALY, B., TÓTH, I. and ERDEI, L.(1978): 2,4-D induced changes in the K^+ uptake of wheat roots at different pH values. — Physiol. Plant. *44*, 395—399.

ZSOLDOS, F. and HAUNOLD, E. (1978): Potassium influx and efflux of 2,4-D and MCPA treated rice plants. — Plant and Soil *49*, 219—228.

ZSOLDOS, F. and HAUNOLD, E. (1978): Herbicide induced changes in the ion uptake of roots at different pH values. — ESNA Newsletter pp. 21—23.

ZSOLDOS, F. and HAUNOLD, E. (1979): Effects of pH changes on ion uptake and 2,4-D influx of wheat roots. — Physiol. Plant. *47*, 77—80.

ZSOLDOS, F. and HAUNOLD, E. (1979): The effects of different concentrations of 2,4-D on the K and P content of wheat. — In: Proc. First Int. Symp. on Mineral Nutrition of Plants. Varna, Bulgaria pp. 275—278.

ZSOLDOS, F. and KARVALY, B. (1979): Cold-shock injury and its relation to ion transport by roots. — In: Low Temperature Stress in Crop Plants. The Role of the Membrane. (Eds. J. M. LYONS, D. GRAHAM and J. K. RAISON) pp. 123—139. Acad. Press, New York.

ZSOLDOS, F. and GULYÁS, S. (1979): Changes induced by chilling in the ion uptake, growth and anatomical structure of rice roots. — Acta Biol. Szeged. *25*, 69—76.

ZSOLDOS, F. and ERDEI, L. (1980): Membrane and ion transport properties in cereals under acidic and alkaline stress conditions. — FESPP Meeting, Santiago de Compostela pp. 742—743.

ZSOLDOS, F. (1981): Gyökér iontranszport változások környezeti stressz hatásokra. (Changes in ion transport of roots under environmental stress effects). — MTA Biol. Oszt. Közl. *24*, 227—238.

ZSOLDOS, F. and HAUNOLD, E. (1982): The effect of 2,4-D on the potassium, ammonium and nitrate ion uptake of rice roots at different pH values. — Physiol. Plant. *54*, 63—68.

ZSOLDOS, F. (1981): Potassium uptake anomaly under H^+ stress in various crop plants. — Plant Physiol. Suppl. *67*, 12.

Strongly selected references

AUDUS, L. J. (Ed.) (1976): Herbicides: Physiology, Biochemistry, Ecology. — Acad. Press, London, New York.

CARSON, E. W. (Ed.) (1974): The Plant Roots and Its Environment. — The University Press of Virginia, Charlottesville.

EPSTEIN, E. (1972): Mineral Nutrition of Plants: Principles and Perspectives. — John Wiley and Sons, Inc. New York, London, Sydney, Toronto.

FRIED, M., TENSHO, K. and ZSOLDOS, F. (1965): Effect of reduced oxygen tension on the uptake of inorganic ions by rice and barley. — In: Isotops and Radiation in Soil-Plant Nutrition Studies (Proc. Ser.). Intern. Atomic Energy Agency, Vienna pp. 233—240.

FRIED, M., ZSOLDOS, F., VOSE, P. B. and SHATOKIN, I. L. (1965): Characterizing the NO_3 and NH_4 uptake process of rice roots by use of N-15 labelled NH_4NO_3. — Physiol. Plant. *18*, 313—320.

INTERNATIONAL POTASH INSTITUTE (1971): Potassium in Biochemistry and Physiology. — Printed by City-Druck AG. Zürich.

LEVITT, J. (1972): Responses of Plants to Environmental Stresses. — Acad. Press, New York, San Francisco, London.

LINSER, H. (1976): The design of herbicides. — In: Herbicides. Physiology, Biochemistry, Ecology (Ed. L. J. AUDUS), pp. 483—505. Acad. Press, New York.

LÜTTGE, U. and PITTMAN, M. G. (Eds.) (1976): Transport in Plants. II. Part B. Tissues and Organs. — Springer-Verlag. Berlin, Heidelberg, New York.

LYONS, J. M. (1973): Chilling injury in plants. Ann. Rev. Plant Physiol. *24*, 445—466.

LYONS, J. M., GRAHAM, D. and RAISON, J. K. (Eds.) (1979): Low Temperature Stress in Crop Plants. The Role of the Membrane. — Acad. Press, New York, London, Sydney.

MENGEL, K. and KIRKBY, E. A. (1978): Principles of Plant Nutrition. — Intern. Potash Inst. Berne. Printed by „der Bund" AG.

SUTCLIFFE, J. F. (1962): Mineral Salts Absorption in Plants. — Pergamon Press, New York, London

Address of the author:
F. ZSOLDOS
Department of Plant Physiology
Attila József University
H—6701 Szeged, P.O. Box 654.
Hungary